POLLINATION BIOLOGY AND THE BREEDING SYSTEM OF *ACACIA RETINODES* (LEGUMINOSAE: MIMOSOIDEAE)[1]

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ABSTRACT

Coastal populations of *Acacia retinodes* Schldl. var. *uncifolia* J. M. Black are protogynous and highly self-incompatible. Flowers are nectarless but insects appear to be attracted to the inflorescences both by the yellow floral color and distinctive fragrance. Neutral red tests suggest that the scent originates from the stigma and epidermal cells of the anthers. Floral foragers represented three insect orders but interpretations of field observations and pollen load analysis of insects indicate that solitary bees in the Colletidae and Halictidae are the major pollen vectors. The method for removal of pollen from the anthers is via thoracic vibration. Because female phase flowers offer no pollen, foraging by bees on such flowers is interpreted as a trend towards partial pollination by deceit.

In Australia, the large number of *Acacia* species (ca. 900, Pedley, 1978, 1979), suggest that this country is a center of speciation and evolution; taken together with the fact that *Acacia* represents the largest genus of angiosperms, we might expect its reproductive biology to be well known. Regrettably, this is not the case. Research into the mechanisms of pollination and seed-setting of Australian species of *Acacia* has been spasmodic and fragmentary. Variation in the number of grains per polyad was documented by Mueller (1887–1888), but it was not until the 1930s that the first cytological studies of pollen germination and pistil interactions were carried out, based primarily on *A. baileyana* F. Muell. (Newman, 1933, 1934a, 1934b). Later, with the advent of electron microscopy, the structural relationships and taxonomic significance of the polyad was established for many species (Guinet & Lugardon, 1976; Guinet, 1981).

Pioneering studies of the breeding system of two Australian species of *Acacia* were carried out at the South African Wattle Research Institute. Philp and Sherry (1946, 1949) established that *A. decurrens* and *A. mearnsii* are only partially self-compatible, and are largely outbreeding. The vectors that assure effective pollination have not been established, although several brief reports have been published suggesting that bees are involved (Armstrong, 1979), or birds in some species (Ford & Forde, 1976). Vogel (1978) considers that *Acacia* is melittophilous.

The question arises whether research into the pollination biology of other mimosoids is further advanced. Arroyo (1981) noted that the basic unit of reproduction in the Mimosoideae is the inflorescence not the individual flower, because the flowers tend to be tiny, numerous, and densely massed. Furthermore, floral sexuality, within a single inflorescence, may intergrade subtly from functionally hermaphroditic through the various forms of decliny (Lewis & Elias, 1981). Therefore, the basic floral morphology of the Mimosoideae offers several obstacles in attempts to interpret pollinator-flower interactions and breeding systems. Modification of the size, floral attractants, and sexuality of the flowers, composing the mimosoid inflorescence, has permitted the exploitation of all animal groups commonly associated with the major trends in pollen dispersal. This includes bees e.g., in *Prosopis* (Simpson et al., 1977) and Mesoamerican *Acacia* (Janzen, 1974); bats e.g., in *Parkia* (Baker & Harris, 1957; Hopkins, 1981); birds e.g., in *Calliandra* (Arroyo, 1981) and *Inga* (Koptur, 1983); and marsupials e.g., in *Inga* and *Acacia* (Turner, 1983). Zoophilous syndromes intergrade in the Mimosoideae. Generalist entomophily occurs in *Acacia macracantha* Humb. & Bonpl. ex Willd. (Zapata & Arroyo, 1978) while some *Inga* spp. are pollinated by hummingbirds and Lepidop-

[1] Research funded by Australian Research Grants Scheme and Australian Department of Education (CPPER); we thank Mr. A. Heisler and rangers of the National Parks Service, Victoria and Mr. C. Campbell for cooperation; Dr. K. Clayton-Greene, Mrs. G. Beresford, Mrs. R. Marginson, and Mrs. B. Wright for assistance; Dr. K. Walker of the National Museum of Vitoria for the identification of Hymenoptera; Ms. J. Gilbert for skilled secretarial assistance; and an unknown reviewer for helpful comments.

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tera (Koptur, 1983). Reliable information pertaining to the breeding systems remains fragmentary and inconclusive. *Neptunia* and *Parkia* are probably self-compatible (Windler, 1966; Baker & Harris, 1957), while self-incompatibility has been tentatively shown to occur in a few neotropical *Acacia* species (Janzen, 1974; Zapata & Arroyo, 1978).

There is therefore an urgent need to explore the reproductive biology of Australian species of *Acacia*. At Melbourne, we have initiated a long-term research program into the role of the polyad in reproduction, using a multi-disciplinary approach. We have established that variation in polyad grain number (4–16 in different species) is matched with ovule number in the ovary (Kenrick & Knox, 1982). However, the polyad grain number/ovule number ratio is very low, 1.2 (Knox & Kenrick, 1983) compared with about 4 in mimosoids with free pollen grains (Cruden, 1977). This suggests that the polyad of *Acacia* has a considerable selective advantage, and is a highly efficient reproductive unit. The compound grains also make for efficient use of available pollinators.

In the present paper, we have investigated the nature of the breeding system in a summer-flowering species of *Acacia, A. retinodes,* and explored its pollinator relationships. We have previously published a preliminary account showing that this species is self-incompatible (Knox & Kenrick, 1983). We now confirm this finding, and relate our results to work on other Mimosoideae.

MATERIALS AND METHODS

Acacia retinodes Schldl. var. *uncifolia* J. M. Black is restricted to coastal sites in South-eastern Australia where it is locally abundant on calcareous sands and is commonly called the Wirilda. Henceforth, in this paper, it is referred to as *A. retinodes*. This study was conducted in an area towards the eastern end of its distribution where *A. retinodes* is a dominant component of the remnants of the coastal flora. Two study sites were chosen at Cape Schanck, Victoria; the first site in the Cape Schanck National Park and the second about 2.5 km away at the Cape Country Club. Both sites are naturally occurring populations.

Breeding system analysis. The peak of flowering of *Acacia retinodes* in the populations at Cape Schanck is from early December until late February; however, occasional trees may be found sparsely flowering at any time of the year. Thirty trees were tested in this study, and each was labelled with a metal tag. Immature flowering shoots containing about three to 15 racemes of inflorescences were enclosed to prevent cross-pollination when the majority of buds were approaching the yellow bud stage (Newman, 1933). Open flowers and phyllodes were removed. The shoots were enclosed in cellulose acetate bags. These were 180 mm by 115 mm in size with 30 mm gussets on either side, and were tied on with plastic covered wire ties. These bags are permeable to air and water molecules, and provide suitable protection from pollinators.

Two or three days later, the shoots were uncovered either for pollen collection, or for pollination. For manipulated pollinations, shoots were trimmed of senescent flowers and unopened buds following the method of Philp and Sherry (1946, 1949). The aim was to pollinate when the maximum number of inflorescences were at the female phase (see Results, Floral Behavior and Dichogamy) with anthers still folded but styles extended.

For each series of crosses, all bagging was done at the same time and five replicate bagged flowering shoots were employed for each type of cross. Several types of pollination were undertaken:

1. Control, pollinators excluded. Because of the small size of the inflorescences, it is quite impractical to emasculate the flowers to prevent accidental self-pollination. Accordingly, to determine whether mechanical autogamy occurred in the absence of pollinators, five samples of flowering shoots on each tree remained bagged during the life of the flowers, i.e., a total of ten to 12 days.
2. Manipulated self-pollination. When the majority of inflorescences in a bag reached early anthesis (see Results for description), the bag was taken off and fully open male phase flowers and unopened buds removed before the inflorescences were self-pollinated. Pollen was applied to the stigmas from the inner surface of 2 ml specimen vials, made of polyvinyl chloride, which had been coated with pollen by pressing fully open flowers against the inside of the vial, to retain only the polyads. The shoots were bagged until the flowers were senescent.
3. Manipulated cross-pollination. These were carried out as described for self-pollinations,

TABLE 1. Variation in number of floral organs in two populations of *Acacia retinodes* at Cape Schanck, Victoria. Explanation of abbreviations: $\bar{x}$, mean; s.d., standard deviation; N, number in sample.

Tree Number:	Population 1				Population 2				Overall Data
	1	3	5	6	20	23	31	34	
A. Number of Flowers/Inflorescence									
$\bar{x}$	22.2	20.2	23.6	21.6	23.0	23.0	30.8	24.2	23.9
s.d.	2.05	0.84	3.44	0.89	1.73	2.86	2.28	2.68	3.73
N	5	5	5	5	5	5	5	5	40 (total)
B. Number of Anthers/Flower									
$\bar{x}$	52.9	56.8	59.2	58.7	62.2	78.0	71.6	72.0	63.5
s.d.	4.03	11.06	7.10	6.03	5.97	8.88	6.08	6.76	10.84
N	25	25	25	19	25	20	25	21	160 (total)
C. Number of Ovules/Ovary									
$\bar{x}$	12.7	13.7	11.9	11.8	12.7	13.2	12.5	12.3	12.6
s.d.	0.82	0.67	0.74	1.03	0.95	1.14	0.53	1.16	1.05
N	10	10	10	10	10	10	10	10	80 (total)

except that the pollen was from another nominated tree.

Pod counting. Pods were counted ten to 28 days after pollination. The number of pods set per infructescence was scored. A comparison was made between pod set following open-pollination and that following controlled pollination in one tree (number 23).

Floral statistics. Data for number of flowers/inflorescence and number of anthers/flower were counted in the laboratory using a high power binocular dissector on fresh or FAA-fixed material. Number of ovules/ovary was observed by fluorescence microscopy after ovaries, dissected from FAA fixed material were stained with decolorized aniline blue (Linskens & Esser, 1957; as modified by Kenrick & Knox, 1981a). The number of polyads/style was scored from open-pollinated, FAA-fixed flowers, which were rinsed in distilled water and stained with Calberla's solution (Ogden et al., 1974) and observed by bright field microscopy. Neutral red staining for detection of osmophores was employed as described by Boyer (1963).

Pollen vector analysis. To determine the pollen vectors of *Acacia retinodes,* insects were selectively collected, from 15 Dec. 1981 to 12 Feb. 1982 from 7:00 A.M. to 4:00 P.M. Collecting periods from 1:00 P.M. to 4:00 P.M. were finally dropped because no insect activity was recorded. Insects were collected *only* when they foraged on the flowers of *A. retinodes.* Foraging is defined here as the active removal of pollen or the probing of floral structures with insect mouthparts. Insects were killed together in jars containing ethyl acetate vapor. To determine the presence of pollen, insects were first observed under dissecting microscopes. To analyze pollen species the same insects were gently pressed against glass slides, to dislodge grains. Samples were stained with Calberla's solution and observed under light microscopy. Because insects had been killed in the same jar there was a continual danger of contamination. Therefore, pollen species were not recorded on a particular insect as present unless 25 individual polyads (for *A. retinodes*) or 25 separate grains (for all other species) could be counted in a single, stained sample. Foraging behavior of insects was noted on *A. retinodes* and on co-blooming species within the study sites.

RESULTS

Floral morphology. The globose inflorescences of *A. retinodes* contain 18 to 34 flowers (Table 1A). Inflorescences are arranged in "racemes" of five to seven inflorescences in the axil of a phyllode; however, at peak flowering, development of the phyllodes is evidently suppressed, and the apices of branches appear to be panicles of globose inflorescences (Fig. 1). After flowering, suppressed phyllodes may develop, and new vegetative growth may occur even from the tips of the racemes.

Each inflorescence bud develops in the axil of a reddish bracteole that ceases expansion at an

FIGURES 1, 2. A flowering shoot of *A. retinodes* var. *uncifolia*.—1. Note that there is usually more than one globose inflorescence per raceme and that inflorescences on the same branch tend to flower acropetally (×0.3).—2. Inflorescence in the female phase (×10).

early stage (Jobson et al., 1985). The calyx has five fused, reduced red sepals and the corolla has five yellow petals, that are reflexed at anthesis. The 34 to 91 stamens in each flower (Table 1B) have anthers that contain eight, 16-grain polyads that dehisce through longitudinal slits (Kenrick & Knox, 1979). The single ovary contains ten to 14 ovules (Table 1C).

The long, narrow style is generally equal to or exceeds the length of the stamens. The terminal cup-shaped stigma is of the wet type (WN) in the classification of Heslop-Harrison (1981). The flowers on most trees examined were hermaphrodite although in 25% of trees, some occasional flowers had undeveloped pistils. No nectaries have been found on the floral axis around the ovary, as occurs in some African species (Robbertse, 1974).

Floral behavior and dichogamy. Inflorescences flower acropetally and the flowers open synchronously within an inflorescence. The majority of styles emerged before 8:00 A.M., and are at first folded in a zigzag pattern, but soon straighten (Kenrick & Knox, 1981a). At this stage, the flower petals are only partially exserted and stamens are compressed beneath the petals. An inflorescence can be said to be truly protogynous since flowering is synchronous. At this point the inflorescence resembles a spiked club, and is referred to as a female phase inflorescence (Fig. 2).

Stamens normally do not fully extend until after mid-day, depending on the weather conditions. When the anther filaments are fully extended the styles are generally hidden. This state marks the beginning of the male phase, although dehiscence usually does not take place until the following day. Rate of floral development may vary according to the prevailing climatic conditions: dry sunny conditions accelerating and cool cloudy weather retarding development.

A fruity odor, reminiscent of ripe cantaloupe melon, is first detectable during the female phase. Neutral red tests for detection of osmophores, during this phase, stain the stigma only. However, scent is most pronounced during the male phase, when the anther epidermal cells stain intensely.

Breeding systems. The data obtained from controlled pollinations demonstrate that *A. retinodes* is highly self-incompatible (Table 2). Cross-pollinations with other trees resulted in high levels of pod set, while self-pollinations gave few or no pods. Higher levels of pod set resulted from interpopulation crosses than intrapopulation crosses.

The self-sterility is almost complete. Control flowering shoots, kept in bags during the flowering period to exclude pollinators showed similar low levels of pod set. In fact, the level is approximately 10% of that of the controlled self-pollinations (Table 2). These controls involved a much larger sample of trees in both populations than the manipulated pollinations. These data indicate that for effective seed set, pollen requires to be transferred from one tree to another. Trees existing very close together, suggesting a common origin from a single parent by root coppicing, were tested for the presence of self-incom-

TABLE 2. Comparison of the breeding systems of two populations of *Acacia retinodes* from Cape Schanck, Victoria following controlled pollinations.

Pollen Source	Number of Trees Tested	Number of Inflorescences Pollinated	Number of Infructescences	Total Number of Pods Set	Pod Set Ratio (4/2)
Female Trees of Population 1:					
Population 1	6	912	209	665	0.73
Population 2	4	581	199	863	1.49
Same tree (selfed)	6	393	4	5	0.013
Control, pollinators excluded	7	3,360[a]	5	12	0.001
Female Trees of Population 2:					
Population 2	8	1,879	320	1,012	0.54
Population 1	3	1,612	355	1,256	0.78
Same tree (selfed)	4	573	12	15	0.03
Control, pollinators excluded	20	4,104[a]	9	37	0.009
Total:	27[b]	13,414	1,113	3,865	0.29

[a] Estimated by using the number of shoots enclosed times 24 (the mean number of inflorescences pollinated per shoot).

[b] Actual number of trees employed.

patibility. In one such system (20A, B, C), the individuals were reciprocally cross-incompatible.

Natural pollination results in significantly lower levels of pod set ($P = 0.001$), than controlled pollination (Fig. 3). Six pods/infructescence were the greatest number set after open-pollination, compared with 13 after controlled pollination on the same tree. It is important to establish the probable frequency of natural pollination to determine the effectiveness of the pollination mechanism(s). Observations of the presence of polyads on random samples of pistils from six different trees showed that there is considerable variation (Table 3), with pollination ratios varying from 0.1 through 0.9, and a mean ratio of 0.37.

Diversity of floral foragers. Floral foragers were active between 7:00 A.M. and noon with the greatest density observed between 8:00 A.M. and 11:00 A.M. Foragers represented three insect orders (Table 4). While dipterans (flies) and hymenopterans (bees) were collected throughout the duration of the field study, coleopterans (beetles) were found visiting flowers only from 15 Dec. 1981 to 4 Jan. 1982.

Native species of solitary bees, and the introduced *Apis mellifera* (feral Caucasian strains) made up more than 70% of the insect collection and were the dominant polyad vectors. Over 55% of the bees collected were *Lasioglossum* (subg. *Parasphecodes*) spp. of the family Halictidae (Table 4).

Insect foraging behavior. Beetles usually ploughed through individual inflorescences in male phase eating pollen and stamens. *Acacia* polyads were deposited sterno- and nototribically with the greatest density confined to the thoracic region. Whole stamens were found in the mandibles of *Stenoderus suturalis* (Coleoptera). Flies landed on inflorescences in male (staminate) and female (pistillate) phase and probed stamens and styles with their probosces. *Acacia* polyads were found infrequently on these insects (Table 5) and were deposited sternotribically on the legs, thorax, and abdomen. Larger bees such as *Lasioglossum* spp., *Apis mellifera,* and *Megachile* sp. landed on inflorescences and crawled over the entire hemisphere continuously scraping the anthers with the two pairs of forelegs and raking with the hind legs. Thoracic vibration was audible at this time suggesting that polyads were harvested by the wing vibration technique as described in *Bombus* (Heinrich, 1976; Bernhardt & Montalvo, 1979) and on other members of the Mimosoideae (Arroyo, 1981). The smallest bees in the genera *Leioproctus* (Colletidae) and *Homalictus* (Halictidae) appeared to visit *each* male phase flower on an inflorescence sequentially. Polyad collection then proceeded as observed for larger bees. *Acacia* polyads were deposited sternotribically on all bee taxa, on the legs, thorax,

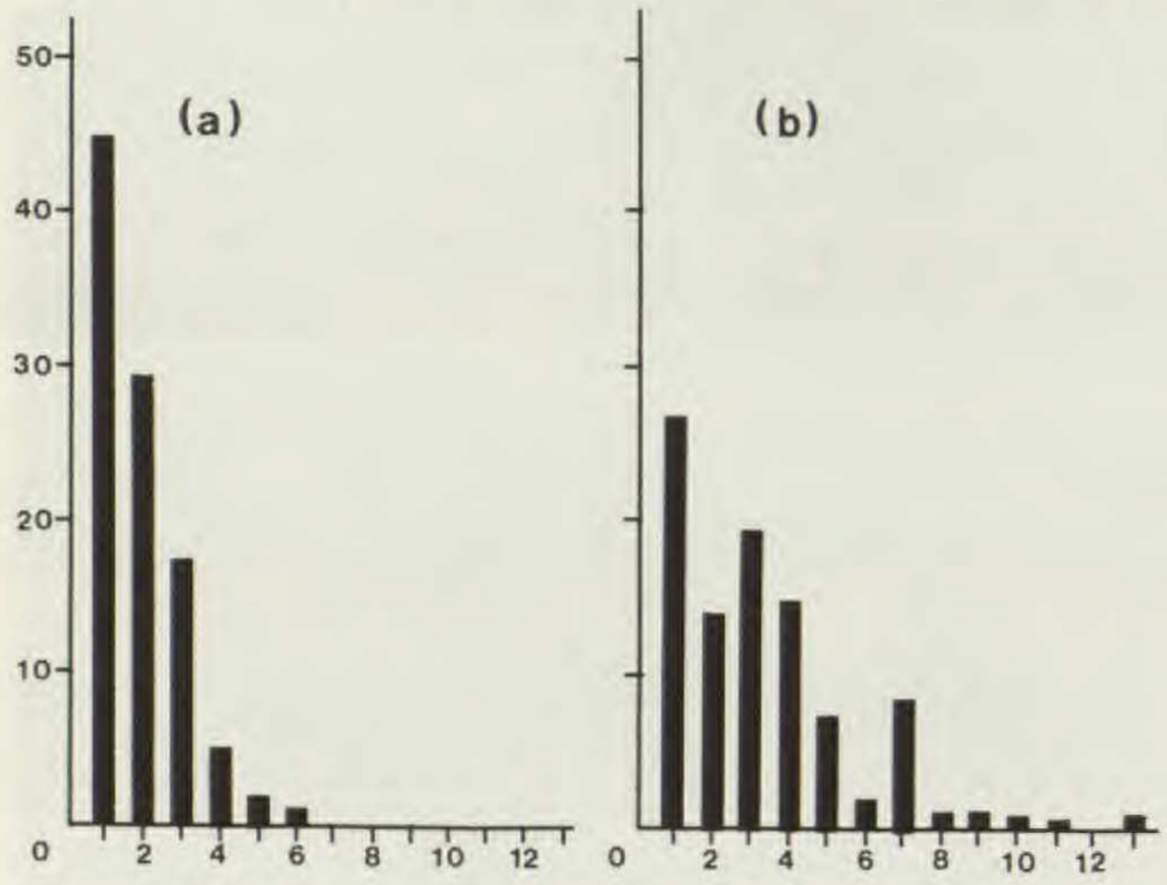


FIGURE 3. Histograms of the percentage frequency of pods set under (a) natural open pollination and (b) manipulated cross pollination on the same tree (number 23). Differences between (a) and (b) are significantly different (D = 7.97, $P = 0.001$).

and abdomen (Fig. 4). Pollen was eventually transferred to the abdomen or scopae of the hind legs of bees (Fig. 5) belonging to asocial families (Colletidae, Halictidae, Megachilidae) or to the corbiculae in *Apis mellifera*.

The amount of time a bee spent on an inflorescence appeared to be directly proportional to the number of flowers in the male phase. *Apis mellifera* and *Lasioglossum* spp. attempted to forage on inflorescences in the female phase but normally abandoned them before covering the full circumference. Small halictids and colletids usually visited all flowers on an inflorescence providing at least one-third of them had just emergent anthers. Undehisced anthers were found in the scopae and corbiculae of all bee taxa collected suggesting that insects did not regularly distinguish between polyads and indehiscent anthers.

Pollinator fidelity and co-blooming plants. Over 62% of bees, the largest group of pollen vectors, carried *Acacia* polyads in association with one or two other species (Table 4). Four pollen species were counted on one *Homalictus brisbanensis* and one *Lasioglossum* (*Parasphecodes*) sp. All bees carrying *Acacia* polyads mixed with the pollen of other species bore, at least, one species of pollen from a flower that also produced nectar (Table 4). A total of eight different pollen taxa were found on insects collected (Table 5). At least four pollen species came from angiosperms that were introduced to Australia and had become

TABLE 3. Frequency of natural pollination of *Acacia retinodes* at Cape Schanck, Victoria.

Tree Number	% of Pistils Pollinated	Number of Pistils Scored
Population 1:		
1	60	90
3	7	114
6	31	96
Population 2:		
20	54	37
23	24	89
34	88	52
Total:	$\bar{x} = 37$	478

naturalized on the Cape Schanck peninsula and throughout Victoria (Willis, 1972).

Bees and flies observed foraging on *Hypochaeris radicata, Lycium ferocissimum, Salpichroa origanifolia,* and *Melaleuca lanceolata* were found to collect nectar from these plants before attempting to remove their pollen. *Hypochaeris radicata* was in flower when the field study began and was collected on insect bodies until 19 Jan. 1982 when its flowering season appeared to conclude on Cape Schanck. The two species of Solanaceae (*L. ferocissimum* and *S. origanifolia*), were also in flower when the field study began and their pollen was found on insects' bodies until the end of the field study. *Melaleuca lanceolata* was not found in flower until mid-January and the first insect bearing its pollen (*Leioproctus metallescens*) was not collected until 18 Jan. 1982.

DISCUSSION

Self incompatibility and the breeding system. The controlled pollination data now reported demonstrate that *Acacia retinodes* var. *uncifolia* is highly self-incompatible. The analysis is based on experiments involving nearly 6,000 inflorescences from trees in two populations. Following self-pollination, less than 2% of inflorescences set any pods; while following intrapopulation crosses, up to 23% of inflorescences set pods, which increased to 34% in interpopulation crosses. All manipulated pollinations were carried out in the field under the same conditions as unmanipulated controls.

A summary of published information on the

TABLE 4. Pollen load analysis of insects collected while foraging on *Acacia retinodes* var. *uncifolia*.[a]

Insect (Order and Species)	Pollen Load			
	Acacia Only	*Acacia* and Other spp.	Other spp. Only	No Pollen
Coleoptera:				
Automolus depressus	—	1	—	1
Belidae	—	—	—	1
Cleobora mellyimules	—	1	—	—
Rhyparida polymorpha	—	—	—	1
Stenoderus suturalis	1	1	—	1
Total:	1	3	—	4
Diptera:				
Eristalis copiosus	1	1	—	—
E. punctulatus	—	2	—	—
Incurviseta sp.	—	—	—	1
Melanguna viridicens	—	1	—	—
Pyrellia sp.	—	1	—	—
Musca vetustissimus	—	—	1	2
Senostoma sp.	—	—	1	—
Stomorhina subapicalis	—	—	—	1
Syrphus damaster	1	—	—	5
Trichareae brevicornis	1	—	—	5
Xanthogramma grandicornis	—	—	1	3
Total:	3	5	3	17
Hymenoptera:				
Anthobosca spp.	—	2	—	1
Apis mellifera	14	4	—	—
Homalictus brisbanensis	8	2	—	—
H. oxoniellus	2	2	—	—
Lasioglossum (*Chilalictus*) sp.	1	—	—	—
Lasioglossum (*Parasphecodes*) sp.	16	52	2	1
Leioproctus metallescens	1	14	—	—
L. plumosus	—	1	—	—
Megachile spp.	—	2	—	—
Total:	42	79	2	2
Grand Total:	46	87	5	23

[a] Combines collections made at both study sites.

breeding system and occurrence of self-incompatibility in *Acacia* and other Mimosoideae is given in Table 6. Very little data are available; only 12 species of *Acacia* and five other genera of Mimosoideae are listed. Data are often brief, and entirely qualitative, and the methods and results are frequently not given. Evidence suggesting the existence of self-incompatibility is given for *A. decurrens, A. harpophylla, A. macracantha, A. mearnsii* and now, *A. retinodes*; and for three other mimosoid taxa, *Calliandra laxa, Enterolobium cyclocarpium*, and *Pithecellobium saman* (Table 6).

Bawa (1974) developed criteria of self-incompatibility: (a) either no more than a third of the individuals are self-compatible and/or (b) cross-pollinations should yield five times more fruit than self-pollinations. Zapata and Arroyo (1978) developed an Index of Self-Incompatibility (ISI), calculated by dividing the average seed set per flower following manipulated selfing, by the results of manipulated cross-pollination. Self-compatible species score >1, while partially self-incompatible species score <1, and complete self-incompatible species score <0.2. In our results with *A. retinodes*, all ten plants that were both

TABLE 5. Pollen analysis of those insects collected bearing *Acacia* mixed with other species.

Insect (Order and Species)	Pollen Species[a]							
	Ac	Hyp	Lyc	Sal	Mel	Pol	Euc	Mal
Coleoptera:								
Automolus depressus	1	1	–	–	–	–	–	–
Cleobora mellyimules	1	1	–	–	–	–	–	–
Stenoderus suturalis	1	–	1	–	–	–	–	–
Diptera:								
Eristalis copiosus	1	–	–	1	–	–	–	–
E. punctulatus	2	–	1	1	–	–	–	–
Melanguna viridicens	1	–	–	–	–	–	–	1
Hymenoptera:								
Anthobosca spp.	2	2	1	–	–	–	–	–
Apis mellifera	4	1	2	–	2	–	–	–
Homalictus brisbanensis	2	1	1	2	–	–	–	–
H. oxoniellus	2	1	–	1	–	–	–	–
Lasioglossum (*Paraspechodes*) spp.	52	17	9	8	28	1	–	–
Leioproctus metallescens	14	–	2	–	12	–	1	–
L. plumosus	1	–	–	1	–	–	–	–
Megachile spp.	2	2	–	–	–	–	–	–

[a] Pollen species: Ac = *Acacia retinodes* var. *uncifolia* J. M. Black; Hyp = *Hypochaeris radicata* L.; Lyc = *Lycium ferocissimum* Miers; Sal = *Salpichroa origanifolia* (Lam.) Baill.; Mel = *Melaleuca lanceolata* Otto; Pol = *Polygala myrtifolia* L.; Euc = *Eucalyptus* spp.; Mal = Unidentified Malvaceae.

self- and cross-pollinated gave overall ratios of self- to cross-pollinated fruit set in populations 1 and 2 of 0.01:0.73, and 0.03:0.57, respectively. This level is also consistent with experimental results from gametophytic self-incompatible cultivars of *Lolium perenne* L. with ratios of 0.26:10.88 pistils pollinated which produced seed (Cornish et al., 1980) and *Trifolium pratense* L. in which only 0.2% of selfed pistils produced seed (Denward, 1963). The overall results with *A. retinodes* give an ISI score of 0.03 on a pod set basis indicating a high level of self-incompatibility; in fact, a score that is seven times lower than required.

The existence of protogyny has now been reported in several *Acacia* spp. e.g., *A. baileyana* (Newman, 1934a), *A. decurrens, A. mearnsii* (Philp & Sherry, 1946), *A. subulata* (Kenrick & Knox, 1981a). Our data extend these observations to *A. retinodes,* and further demonstrate the existence of a female phase at stigma exsertion which is especially favorable for cross-pollination. In this summer-flowering species, the female phase is coincident with the period of greatest activity of insect pollinators, and may be as short as 2–3 hr. Pollinations made following days of temperatures >30°C show drastically reduced pod set (Kenrick & Knox, unpubl. data). It appears that high temperatures may intensify the expression of self-incompatibility in the stigma and style, or make pollen inviable or stigma unreceptive. The data indicate that for successful pod set, pollen must be transferred from one tree to another.

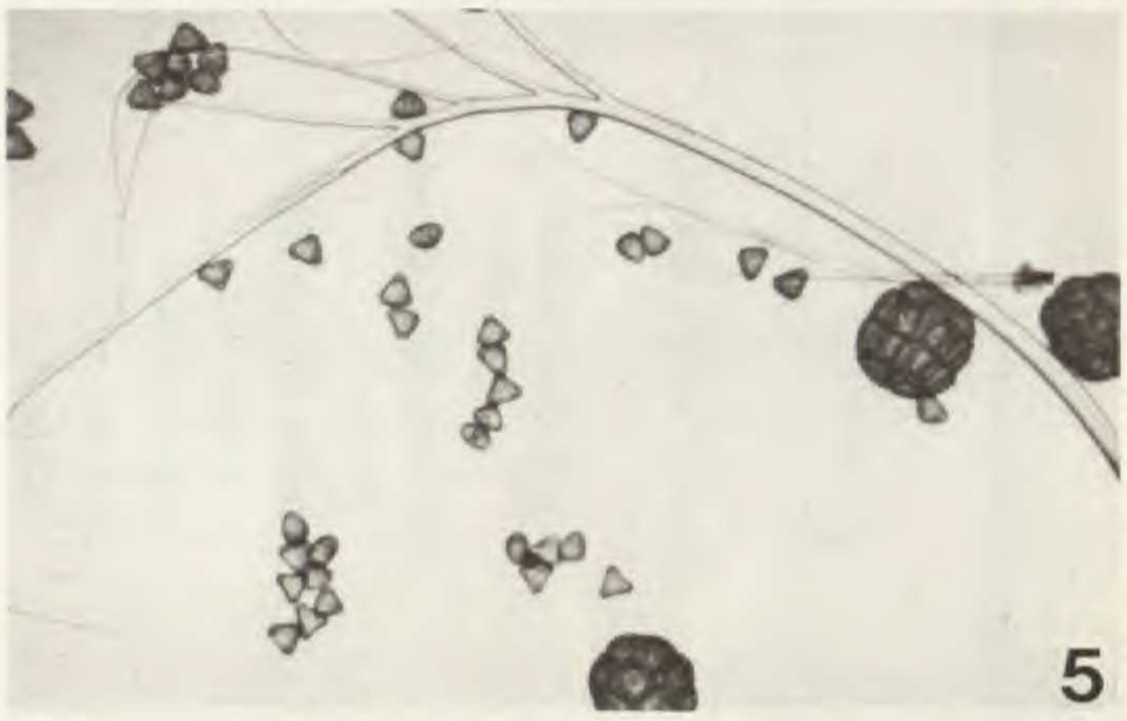
Pollination biology of Acacia. Bees appear to be the only consistent pollen vectors of *A. retinodes* despite the presence of other floral foragers representing two more insect orders. *Acacia retinodes* should be regarded as a "generalist" mellitophile, as pollinating bees span three native families of solitary Apoidea as well as the naturalized, eusocial *Apis mellifera* (primitively eusocial Halictidae do not occur in Australia; C. D. Michener, pers. comm.). These results parallel observations by Janzen (1974) concerning the swollen thorn acacias of Mesoamerica. Although the polyads of *Acacia* are not shed, as in annonalian or aroid taxa (Vogel, 1978), they do protrude during dehiscence and remain exposed on the surface of the anther (Kenrick & Knox, 1979). This should encourage generalist entomophily as in the American *Prosopis* species (Simpson et al., 1977; Arroyo, 1981), as specialized foraging hab-

its are not required to remove polyads from dense, brushlike inflorescences. *Acacia retinodes,* though, receives a less varied spectrum of pollinators than *Prosopis* as it lacks floral nectaries. *Acacia retinodes* is of little interest to moths, most butterflies, wasps, carrion, and dung flies etc. that do not require the protein and lipids in pollen for ovulation or as a food source for larvae. Post-pollination exudate is not a nectar substitute! Secretions occur very briefly *after* pollination has occurred and if insects were attracted to the fluid they would undoubtedly interfere with the polyad-stigma interface (Kenrick & Knox, 1981b).

Furthermore, female phase inflorescences of *A. retinodes* offer no edible reward but they do offer color and scent as floral attractants. Cross-pollination must occur most frequently via "partial pollination by deceit" (sensu Vogel, 1978; Bernhardt & Montalvo, 1979). The discrepancy between natural and artificial (hand-pollinated) pod set may be based in part, on the foraging of bees that learn to discriminate between male and female phase inflorescences. Bees typically do not visit all of the flowers on a female phase inflorescence but an objective, artificial cross-pollination will probably result in a higher number of successful fertilizations.

Self-incompatibility undoubtedly limits the success of pod set between siblings or parents and their progeny. Interpopulational crosses are, therefore, superior to intrapopulational crosses. Long distance pollinations seem most unlikely with primary pollinators belonging to the Halictidae and Colletidae. Ironically, if such pollinations occur naturally in this region, they would be effected only via the "trap-line" foraging of the introduced honeybee!

Is natural seedset lowered in *A. retinodes* by competition for pollinators with so many naturalized plant species? Simpson et al. (1977) and Arroyo (1981) suggested that the most efficient bee pollinators of many Leguminoseae were those with polylectic-oligolectic (not monolectic) foraging patterns. This increases the frequency of cross-pollinations as small bodied bees, dependent on only one plant species for pollen, rarely visit more than one large shrub during a foraging bout. Narrow polylectic foraging seems to be the norm in bees associated with Australian *Acacia* species as these insects must obtain their chemical energy (floral nectar) from co-blooming taxa (Bernhardt, 1983; Bernhardt & Walker, 1983a, 1983b). The only established competitor for the



FIGURES 4, 5. 4. Ventral view of *Leioproctus metallescens* caught on *A. retinodes* showing the build-up of pollen on the hind legs and abdomen in contrast to the forelegs and thorax (×9.4).—5. Scopal hair of *Lasioglossum* (*Paraspechodes*) sp. bearing a mixed load of polyads of *A. retinodes* and grains of *Melaleuca lanceolata* (×640).

pollinators of an *Acacia* species is another *Acacia* species (Bernhardt, 1983; Bernardt & Walker 1983a). True "pollen flowers" (sensu Vogel, 1978) have overlapping flowering periods with sympatric, nectariferous plants pollinated by the same bees (Heinrich, 1976; Bernhardt & Montalvo, 1979; Bernhardt, 1984). This has been interpreted as selectively advantageous as the limited pollinator resource is shared. It seems most likely that the invasion of European and South African plants has not put pressure on *A. retinodes* but has supplanted the original nectar flora, excluding *Melaleuca lanceolata* (Willis, 1972).

Unlike the majority of mimosoids studied so far, *Acacia retinodes* should be regarded as a "Papaver Type" pollen flower (sensu Vogel, 1978) due to the absence of floral nectaries and the accessibility of polyads retained on the anthers. Self-incompatibility and synchronous protogyny encourage cross-pollination in *A. retinodes* but also reduce the success of bee-mediated geitonogamy. The absence of floral and extra-floral nectar reduces the spectrum of potential pollen

TABLE 6. Breeding system of selected species of *Acacia* and other genera of Mimosoideae.

Species	Interpretation[a]	Number of Trees Sampled[c]	Number of Flowers Tested per Pollination per Tree[c]	Pollination Tests[b,c]	Reference
1. *Acacia*					
A. aroma Hook. & Arn.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
A. constricta Benth.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
A. cornigera L.	outbreeding	NG	NG	seed set in glasshouse	Janzen, 1974
A. decurrens Willd.	outbreeding	14	flowering branches, 8.3/tree	open 71.9%, self 26.8%, 400 ovules/tree	Philp & Sherry, 1946; Moffett & Nixon, 1974
A. drepanolobium Harms. ex Sjöstedt	SI	42	NG	seed set in glasshouse	Hocking, 1970
A. furcatispina Burk.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
A. greggii Gray	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
A. harpophylla F. Muell. ex Benth.	outbreeding	17	NG	number of pods/cluster, cross 0.47%, self 0.19%–0.26%	Coaldrake, 1971
A. macracantha H. & B.	SI	6–7	3,786–15,780	cross 0.19%, self 0%, control 0%	Zapata & Arroyo, 1978
A. mearnsii De Wild. (syn. *A. mollissima*)	outbreeding	24	flowering branches	number of viable seeds/pod, open 6.8%, self 2.7%	Moffett, 1956
2. Other Mimosoidea					
Calliandra laxa Benth.	SI	5–6	136–139	cross 11.76%, self 0%, control 0%	Zapata & Arroyo, 1978
C. eriophylla Benth.	SI	>1	1 flowering branch	NG	Simpson, 1977

TABLE 6. Continued.

Species	Interpretation[a]	Number of Trees Sampled	Number of Flowers Tested per Pollination per Tree	Pollination Tests[b]	Reference
Enterolobium cyclocarpum (Jacq.) Griseb.	SI	3–5	15–100	number of flowers setting seed, self 0%, cross 0.28%	Bawa, 1974
Leucaena trichodes (Jacq.) Benth.	SI	NG	NG	NG	Hutton & Eddie, 1982
L. esculenta (MCC & Sesse) Benth.	SI	NG	NG	NG	Hutton & Eddie, 1982
L. collinsii Britton & Rose	SI	NG	NG	NG	Brewbaker, 1982
L. lanceolata S. Watson	SI	NG	15	NG	Brewbaker, 1982
L. macrophylla Benth.	SI	NG	4	NG	Brewbaker, 1982
L. pulverulenta (Schlecht.) Benth.	SI	NG	18	NG	Brewbaker, 1982
L. shannoni Donn. Smith	SI	NG	15	NG	Brewbaker, 1982
Pithecellobium saman Jacq.	SI	3–5	15–100	self 0%, cross 0.28%	Bawa, 1974
Prosopis chilensis Mol. Stuntz emend. Burk.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
P. flexuosa DC.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
P. velutina Woot.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
P. torquata (Lag.) DC.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977

[a] SI = self-incompatible.
[b] Control pollinations: inflorescences bagged but unmanipulated.
[c] NG = not given.

vectors, excluding vertebrates like arboreal marsupials (Turner, 1983) and birds (Ford & Forde, 1976; Kenrick et al., 1983), but it may also encourage cross-pollination as bees are forced to leave individual plants periodically when their supply of chemical energy is depleted.

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